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Editors:

A. Seetharam K.W. Riley G. Harinarayana



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ORIGIN, EVOLUTION AND SYSTEMATICS OF

JMJ de Wet

The Poaceae includes an estimated 8,000 species belonging to some 600 genera. Grasses occur on all continents, and in all habitats that support growth of flowering plants. They serve man in many ways, but it is their use as cereals and feed for livestock that make them essential for human survival. The caryopses of most grasses are edible, and at least 300 species were harvested during historical times as wild cereals by nomadic hunters and herders, and by farmers during times of scarcity. Thirty five species belonging to 20 genera are known to have been domesticated. Their cultivated races rely on man for seed dispersal (sowing), and for a suitable habitat to reproduce successfully (cultivated field).

Cereals are globally planted on an estimated 730 million hectares, and yield an estimated 1,800 million metric tons of grain annually Wheat, maize and rice account for approximately 80 per cent of grain produced in the world These cereals are followed in importance by barley, sorghum, oats, rye and pearl millet which together represent another 19 per cent of the world's cereal production. The remaining cereals account for about 1 per cent of the foodgrain produced in the world today. These mirror cereals are not important in terms of world food production, but essential as food crops in their respective agroecosystems. They are mostly grown in marginal areas, or under agricultural conditions where major cereals fail to consistently produce an acceptable harvest.

MINOR CEREALS OF THE AMERICAS

Wild cereals played an important role in the diets of native Americans until recent historical times (Palmer, 1871, Ball, 1884). Fifty species were extensively

harvested, but only six species were domesticated as cereals. Maize (Zea mays L.) is the only New World cereal of commercial significance. Setaria geniculata (Lam.) P. Beauv. (brittle grass) from and Mexico (Callen, 1965), and Phalaris caroliniana Walt. (may grass) of the southeastern United States (Chomko and Crawford, 1978) are known as cultivated cereals only in an archaeological context. Brittle grass was grown for at least a millennium (Callen, 1967), but was replaced by maize as a cereal some 4000 years ago. (Mangelsdorph, MacNeish and Gallinat, 1967). Two minor cereals, mango. (Bromus mango Desv.) in Chile and sauw. (Panicum sonorum Beal) in Mexico were important crops until recent historical times. American wild nice. (Zizania acquatica L.) is a recent domesticate in north central Canada and adjacent regions of the USA. (de Wet and Oelke. 1979).

Molina (1782) recorded that the Araucano Indians in Central Chile grew a kind of type that was called el Mango, and a kind of barley that was called Tuca. Tuca probably refers to Bromus unioloides HBK, a wild grass that Extensively harvested as a cereal on the highlands of South America (Ball, 1884). El Mango (Bromus mango) was cultivated Gay (1865) recorded that it was a biennial crop, grown with peppers and beans. Florets were roasted to facilitate removal of the lemma and palea, and the grains were ground into flour to make bread or a fermented drink called chicha. Cruz (1972) cited an unpublished manuscript by Arturo Fontecilla Larrain, a professor of agronomy at the Catholic University of Santiago in Chile during the early twentieth century, who recorded that plants of el Mango produced 40-50 culms, each bearing an inflorescence with 70-100 grains. It required eighteen months to mature, however, and el Mango was replaced during the last half of the twentieth century by wheat for making flour and by apples to make cider (Brucher, 1979).

Sauw (Panicum sonorum) is native to arid western North America. It formed an important part of the Sonoran desert agriculture of northwestern Mexico (Nabhan and de Wet, 1984). It was widely grown well into the twentieth century by Indian tribes who lived along the Colorado river delta (Gifford, 1931). Today it is grown only in southeastern Sonora and adjacent Chiuahua Although little known outside this gree, sauwi is a promising cereal for the semi arid tropics of Africa and Asia. It is drought tolerant, and has acceptable yield ential under adverse conditions. Plants produce several tillers, each of which duce an inflorescence with as many as 2.500 fertile florest.

The only New World minor cereal of present-day economic importance is American wild rice. This is not a true rice. It belongs to the genus Zizania rather than Oryza. American nce is commercially harvested as a wild cereal (Dore, 1969), and since the late 1960's planted on a commercial scale Zizania acquatica is the only grass species successfully domesticated as a cereal in historical times (de Wet and Oelke, 1979). It is grown in paddies as is rice. Paddies are flooded and seeded in late fall. Germination is rapid in spring and the water level is maintained until August when the crop matures. Fields are

then drained and harvested with a modified rice combine. Since the cultigen retains some degree of natural seed dispersal, no subsequent sowing is needed Spikelets and straw are worked into the wet soil after harvest, where the caryopses he dormant until the soil thaws in the next spring. Natural populations rarely yield more than 100 kg ha⁻¹, while yields of 1000 kg ha⁻¹ are obtained in planted paddies. Yields of at least 3000 kg ha⁻¹ are possible from fully non-shattering cultivars.

MINOR CEREALS OF AFRICA

At least 60 grass species were extensively harvested in Africa as wild cereals until recent historical times (Busson, 1965, Jardin, 1967). The widely distributed Brachiana deflexa (Schumach.) C.E. Hubbard, Oryza barthii A. Chev., and Paspalum scrobiculatum. L. were extensively collected in West Africa. Stipagrostis pungens (Desf.) de Winter, and Cenchrus biflorus Roxb were harvested by nomadic tribes in the Sahara. These species are often still encouraged as weeds in cultivated fields where they are harvested as wild cereals.

In West Africa, Oryza barthii Chev gave rise under domestication to the cultivated O glaberrima Steudel (Porteres, 1976) Teff, Eragrosis ief (Succ.) Trotter, is an important cereal in the Ethiopian highlands and was probably derived from E pilosa (L.) P. Beauvois (de Wet, 1977, Costanza, de Wet and Harlan, 1979). The weedy Brachiaria deflexa (animal fonio) is cultivated on the Fouta Djakon highlands of the west African savanna (Chevalier, 1933, Proteres, 1951). Animal fonio differs from wild B deflexa only in having spikelets that disarticulate tardily at maturity.

Two other minor cereals are important crops in the west African savanna Black fonio. Digitaria iburua Stapf is grown by the Hausa tribe of Nigeria, and occurs sporadically across most of semi-arid west Africa (Porteres, 1955, Clayton, 1972). It is often planted between rows of sorghum or pearl millet, and commonly as a mixture with Digitaria exilis (Kippist) Stapf (true fonio) Black fonio (D burua) is drought tolerant and often yields a harvest when the major cereal it accompanies fails to survive. True fonio (D exilis) is widely grown across the west African savanna. It differs from D iburua which has both glumes conspicuously shorter than the spikelet, in having the upper glume at least as long as the spikelet. Fonios are sown in west Africa during May or June, and harvested in September. Harvested inflorescences need to be protected from moisture since the grains become agglutinated to the lemma and palea when they get wet. Threshed grains are parched or dried in the sun before the chaff is removed by pounding in a wooden mortar. Fonio is used in stews, or the boiled grains are eaten as nice with butter or palm oil used.

The most important minor cereal in Africa is finger millet, Eleusine coracana (L.) Gaertner. It was domesticated in Africa, but is also widely grown in south

Asia, particularly India (Hilu and de Wet, 1976a) The closest wild relative of finger millet is *E coracana* subsp *africana* (Kennedy-O'Byrne) Hilu and de Wet Spontaneous finger millet is widely distributed along the eastern and southern highlands of Africa (Phillips, 1972) Derivatives of hybrids between cultivated and wild taxa are companion weeds of finger millet across most of its distribution in Africa

Finger millet first occurs in the archaeological record of early African agriculture dating back some 3,000 years (Hilu and de Wet, 1976b), and was introduced into India at least 3,000 years ago (Vishnu-Mittre, 1968). Cultivated finger millet is extensively variable, and this variation is recognized as five races by de Wet, Prasada Rao, Brink and Mengesha (1984). Race coracana is widely distributed across the range of finger millet cultivation in Africa and Asia. It resembles wild finger millet in having five to nineteen slender inflorescence branches that are 6-11 cm long, digitately arranged, and with the tips often becoming slightly incurved or reflexed at time of maturity. Some genotypes differ phenotypically from subsp. africana primarily in being unable to disperse their spikelets without the help of man. Race coracana is particularly well adapted to agriculture in the eastern highlands of Africa and the Ghats of India. Some cultivars are drought tolerant and compete aggressively with weeds under conditions of traditional agriculture. It is often sown as a secondary crop with sorghum or pearl millet.

Races vulgaris, elongata, plana and compacta probably evolved from race coracana under cultivation. They probably evolved in Africa and were introduced into India. Little racial evolution took place in this secondary centre of cultivation. Race elongata is characterized by slender inflorescence branches that are 10-24 cm long. It is grown in eastern Africa and the eastern Ghats of India Indian and African cultivars cannot consistently be separated on the basis of inflorescence morphology. Race plana is primarily African in distribution. It is grown in Ethiopia and Uganda, and to some extent in the eastern and western Ghats of India Race plana is characterized by large, 8-15 mm long spikelets that are arranged in two more or less regular rows along the rachis, giving the inflorescence branches a flat ribbon-like appearance. In some genotypes the fertile florets are so numerous that they almost surround the rachis at maturity. These genotypes somewhat resemble race compacta. except that the inflorescence branches are not incurved. Members of race compacta are known as cockscomb finger millets in both Africa and India Spikelets are up to ten flowered, with the inflorescence branches divided at the base and strongly incurved to form a fist-like inflorescence. Indian cultivars commonly have an inflorescence branch located some distance below the terminal cluster on each primary inflorescence axis. African cultivars usually lack this lower inflorescence branch. Race compacta is grown in northeastern India, Ethiopia and Uganda

Race vulgars is the most common finger millet of Africa and Asia. It is grown in Africa from Uganda to Ethiopia and to south Africa, and in Asia from India to Indonesia Inflorescence branches are twisted or incurved Some genotypes are drought tolerant, others are well adapted to areas of high rainfall. and still others are sown in nurseries and transplanted to fields with the first rains of the season. In rice growing areas race vulgaris often follows irrigated rice as a rabi crop Grains are cooked as rice, or ground into flour to make porridge or unleavened bread

MINOR CEREALS OF EURASIA

Ten minor millets are grown in Asia. Their survival as cereals in competition with rice and wheat attests to the significance of these cereals in the agroecosystems of Asia. Two of these. Panicum miliaceum L. (broomcorn or prosomillet) and Setaria italica (L.) P. Beauv. (foxtail millet) are grown across temperate Eurasia, with foxtail millet extending into the semi arid tropics of Asia Other minor cereals are important in specialized agricultural niches in Asia

Crabgrass or manna Digitaria sanguinalis (L.) Scop is a common weed in all temperate parts of the world. The species is morphologically variable and variously classified into subgenera and varieties (Gould 1963). It is an annual grass with prostrate or decumbent stems and flowering culms that can reach well over one metre in height. The species was harvested as a spontaneous semi domesticate is southern Europe until the first quarter of this century (Werth, 1937) It is cultivated as a cereal in the Caucasus and Kashmir (Henrard 1950 Bor 1955) Craborass has been a crop for at least 2,000 years. Plinius who lived in the first century A.D. referred to the species as ischaemon and suggested that it was of Slavic origins (Kornicke and Werner 1885) Matthiolus (1565) recorded that this cereal was grown in Bohemia Slavonia and the Ukraine Kornicke and Werner (1885) reported that in Hungary one hectare yielded 420 520 kg of grain and 780 1200 kg of hay During the late nineteenth century the species was an important cereal in southeastern Europe (Ascherson and Graebner 1890) Wild manna was harvested with a sickle before the plants were fully matured (Becker Dillingen, 1927) It never lost the ability of natural seed dispersal. Little is known about its present cultivation in the Caucasus and Kashmir

Another crabgrass, Digitaria cruciata (Nees) A Camus, is cultivated by the Khasi tribes in Assam, where it is known as raishan. Hooker and Stapf (1896) recognized this cereal as a species of Paspalum and Bor (1940) mistakenly included it in Digitaria corymbosa (Roxb.) Merrill. Bor (1955). correctly transferred raishan to D cruciata and recognized the cultivated kinds as var esculenta Bor Veldkamp (1973) described var pectinata Veldkamp to include a cultivar with clutinous grains that was grown at Cha Pa in northern Vietnam

Raishan is an annual grass with prostrate to decumbent culms that root at the lower nodes, and that produce flowering culms up to 1.3 m tall Inflorescences consist of two to ten racemes arranged on a 1.4 cm long certal axis, with the racemes up to 18 cm long reflexed at maturity. The chartaceous lemma and palea tightly enclose the grain at maturity, but the grain is readily freed from this fruitcase by pounding in a mortar.

Raishan persists as a cereal in Assam probably because it provides excellent and essential feed for livestock during winter when grazing is scarce. It is commonly sown on land from which potatoes or other crops have been harvested. It is planted between early April and late. June and harvested in November. In October the culms are tied together into bunches and allowed to mature. Individual plants produce as many as 30 flowering culms with each inflorescence maturing at a slightly different time. Spikelets are collected by hand about a month after the main inflorescence matures (Singh and Arora, 1972). Harvested spikelets are dreid in the sun before they are stored, and usually parched over a fire before they are pounded in a mortar to remove the lemma and palea. The cleaned grains are boiled in a mixture with rice. Singh and Arora (1972) reported that raishan yields up to 800 kg ha. 1. The species was probably domesticated by hill tribes in Assam and southeast Asia.

The genus Echinochloa is widely distributed, and includes some 20 species several of which are aggressive weeds. The most obnoxious weed is Ecoryzoides (Ard.) Firstsch. It invades paddy rice, mimics the crop in vegetative morphology, and flowers a few days earlier than the cultivar it accompanies as a weed. Natural seed dispersal before the crop is harvested, and seed dormancy ensure a new population of Echinochloa weeds when rice is planted in the same field during the next growing season.

Barnyard millet, E crusgalli (L.) P. Beauv is a common weed of temperate and warm regions of the Old and New Worlds. The species is cultivated in China, Korea and Japan, where it is commonly known as Japanese millet Archaeological records indicate that it was grown in Japan during the Yayoi period dating back some 5.000 years (Watanabe, 1970). Cultivated plants are erect, tufted annuals up to 1 m tall. Inflorescences are erect or slightly bent at maturity, with the ascending racemes often incurved at the tip. Spikelets are persistent and typically cuspidate.

The related Echinochloa colona (L.) Link was harvested as a wild cereal in predynastic Egypt (Dixon, 1969). Intestinal contents of mummies excavated at Naga ed-Der include, among other plant remains, recognizable grains of E. colona. It is a minor wild cereal in Central Africa where the grains are fermented to make beer (Tisserant, 1953). This cereal has as yet not been identified from among plant remains of the numerous farming sites excavated in India (Vishnu-Mittre, 1977). The species is, however, extensively grown in central India where it is commonly known as sawa (de Wet et al., 1983a).

Sawa differs from Japanese millet primarily in being a more tropical grass, and in lacking the beak to the spikelet that characterizes E crusgalli. Both species have 2n=54 chromosomes but hybrids between them are strille (Yabuno 1966). Sawa is an indigenous cereal in India. The species is weedy, spontaneously invades cultivated fields, and is often unintentionally harvested with other minor millets. Sawa is grown in India from Kashmir to Sikkim in the north, and to Tamil. Nadu in the south. Cultivated kinds are extensively variable (de. Wet et al., 1983a). The strongly branched racemes of some cultivars suggests affinities with Japanese millet, but E crusgalli does not occur in India as a cereal.

Kodo millet Paspalum scrobiculatum L, is another indigenous cultivated cereal of India. The species is widely distributed in damp habitats across the tropics and subtropics of the Old World. It is known to have been grown in southern Rajasthan and Maharashtra for at least 3,000 years (Kajale, 1977). It is grown today from Uttar Pradesh to Bangladesh in the north, and Kerala and Tamil Nadu in the south. This cereal is known as kodo in Hindi and varagu in Tamil. A small seeded and large seeded kind are recognized by farmers in Tamil. Nadu.

Raceme morphology allows for the recognition of three cultivated complexes. The most common kodo millets are characterized by racemes with the spikelets arranged in two rows on one side of a flattened rachts as is also typical of wild P scrobiculatum. Two variations on this spikelet pattern often occur in the same field as the more common phenotype. In the one complex, spikelets are arranged in two to four irregular rows along the rachs. In the other complex, the lower part of each raceme has four irregularly arranged rows of spikelets while spikelet arrangement becomes more regularly two rowed in the upper part of the raceme (de Wet et al. 1983b). Hybridization between cultivated kinds, and between weedy and cultivated races is common. This explains the absence of clear racial differentiation, even after some 3 000 years of cultivation as a cereal in India.

Farmers believe that kodo millet is poisonous after a rain. It is known to produce unconsciousness, or delirium with violent tremors of the voluntary muscles. Kodo millet is cooked as rice. Bhide and Aimen (1959) suggested that the glumes, lemmas and paleas contain poisonous alkaloids. It is more likely that the poisoning results from a fungus that often invades and eventually replaces the developing grain. The spore masses are about the same size as mature grains and are not easy to detect at harvest time. Removing the husks and winnowing scatter the spores, and only healthy grains remain to be used as food. Poisoning only occurs when the grains are damp at threshing, and the spores are not winnowed away.

Adlay, Coix lacryma jobi L., is grown under shifting cultivation as a rainfed crop by the hill tribes of tropical Asia from Assam to the Philippines (Arora,

1977) The grains of wild adlay are enclosed in indurated involucres. Wild C lacryma-jobi is called Job's tears, and the involucres of wild taxa are used to make rosaries and necklaces. Involucres are paperly in most cultivars allowing for the ready removal of the grain. In Assam, the grain is ground into flour, and used to make bread, or a sweet dish is prepared by frying the grain and adding sugar. The whole grain is also eaten raw as a snack, or fermented to produce beer.

Two minor millets, Setaria pumila (Poir) Roem and Schult, and Brachiana ramosa (L.) Stapf, are indigenous as cereals to the hills of central India. As wild species, however, they are widely distributed in tropical Africa and Asia. Cultivated kinds are distinguished from their close wild relatives only in the absence of efficient natural seed dispersal. Complexes with various degrees of spikelet disarticulation commonly occur in the same field. Both species often occur as encouraged weeds in fields of finger or foxtall millets.

Two Eurasian cereal species are of commercial importance. These are Setaria Italica (L.) P. Beauv. (foxtail millet), and Panicum millaceum L. (broomcorn millet). Both species are extensively grown across temperate Eurasia, with foxtail millet extending into the tropics and sub tropics of Asia.

The closest wild relative of foxtail millet is the weedy green foxtail, Setaria Italica subsp. viridis (L.) Thellung. Green foxtail is native to temperate Eurasia, but was introduced and became widely established as a weed in temperate parts of the Americas. Wild and cultivated S. Italica cross naturally to produce fertile hybrids (Li, Pao and Li. 1942, Li, Li and Pao, 1945, de Wet. Oestry-Stidd and Cubero, 1979). Derivatives of such hybrids are obnoxious weeds in the American corn belt. (Pohl. 1966).

The antiquity of foxtail millet cultivation is uncertain. The species could have been domesticated anywhere across its natural range extending from Europe to Japan. It has been grown in China for at least 5,000 years (Ho, 1975). Jars filled with husks of foxtail millet were found at Ban po in Shaniy province dating from the Yang shao period (Nai, 1963, Chang, 1973). Foxtail millet also occurs in early agricultural sites from Switzerland and Austria dating back some 3,000 years (Werth, 1937). The species became widespread as a cereal in Europe during the Bronze age (van Zeist, 1970). It is absent from known early farming sites in India (Vishnu-Mittre, 1968). This, however, does not necessarily indicate a late introduction of foxtail millet into the tropics and subtropics of South Asia. Its wide distribution and morphological variation suggest a long history of cultivation in tropical Asia.

Foxtail millet is commonly classified into a European complex (race moharta) and a Far Eastern complex (race maxima). Race moharta includes cultivars with relatively small and erect inflorescences (Kornicke and Werner, 1885), while race maxima is characterized by large and pendulous inflorescences (Dekaprelevich and Kasparian, 1928). Two inflorescence types

of race maxima are recognized by Gritzenko (1960). Plants with small, essentially erect, and compact inflorescences occur in northwestern China and Mongolia. Plants from eastern China, Japan and Korea typically have large, compact, and pendulous inflorescences. Cultivars from India are morphologically distinct from those of Europe and the Far East, and are recognized as race indica by Prasada Rao et al. (1987). Plants are typically robust, with inflorescences bearing branches that are loosely arranged along the primary axis. Some collections from northern India resemble race maxima and probably represent introductions from China. Collections from Meghalaya have long, siender inflorescences with small spikelets. Two collections of the International Crops Research Institute for the Semi Arid Tropics (ICRISAT) from Karnataka have siender, erect, inflorescences with short lateral branches, somewhat resembling S. pumila in inflorescence and spikelet structure. These collections, however, have one to three bristles below each spikelet, whereas S. pumila has four or more bristles supporting each spikelet.

The progenitor of broomcorn millet (Panicum miliaceum) is native to Manchuria. The species was probably introduced into Europe as a cereal at least 3,000 years ago. Spikelets and florets of broomcorn millet occur together with remains of foxtail millet in early farming sites of the European neolithic Neuweiler (1946) dated these sites to around 1600 B.C. During the Bronze age the species rapidly spread across Europe as a cereal (Hjelmquist, 1955)

Cultivated kinds of *P miliaceum* are commonly subdivided into five subspecies (Lyssov, 1975). These are here recognized as races without taxonomic validity. Race miliaceum resembles wild *P miliaceum* in inflorescence morphology. It is characterized by large, open inflorescences with suberect branches that are sparingly subdivided. Race patentissimum with its slender and diffused panicle branches is often difficult to distinguish from race miliaceum. These two races occur across the range of broomcorn millet cultivation from eastern Europe to Japan. Highly evolved cultivars of broomcorn millet have more or less compact inflorescences. These are classified into races contractum, compactum and ovatum. Cultivars included in race compactum have cylindrical shaped inflorescences that are essentially erect. Cultivars with compact and slightly curved inflorescences that are ovate in shape are included in race ovatum.

Races have no ecogeographic unity. This probably is due to extensive movement of seed of the crop across Eurasia, particularly since early in this century. Lyssov (1975) illustrated 21 inflorescence types that are commonly grown in Eurasia.

A different Panicum species (sama) is grown as a cereal in the eastern Ghats of India (Rangaswami Ayyangar and Achyutha Warier, 1941). This species. P sumatrense Roth ex Roem and Schult, represents the

domesticated complex of the weedy P psilopodium Trin (de Wet, Prasada Rao and Brink, 1984) The commonly cultivated kind differs from wild P psilopodium with which it crosses to produce fertile hybrids, primarily in having lost the ability of natural seed dispersal. This race of sama is highly tolerant to heat and drought stress. In more favourable agricultural habitats of the eastern Ghats a robust race of sama is grown. The inflorescences of this race are strongly branched and compact. Sama is often grown as a mixture with foxtail millet, pearl millet or sorghum.

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